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A CASE OF POLYMORPHISM IN ASPLANCHNA SIMULATING A MUTATION

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DURING the fall of 1909 the writer accidentally discovered a case of heterogenesis in the genus *Asplanchna* which bore all the earmarks of a bona fide mutation. The two forms concerned were quite sufficiently different to be classed as distinct species, and even as strongly marked species. The transition was sudden and complete, without apparent intergradation. The transition was also in one direction only, and it could not be considered as in any sense due to an immediate cross, because the reproduction of the *Asplanchna,* aside from resting eggs, is wholly parthenogenetic.

Subsequent study of the same species, during the following spring, as it appeared in several different locations, supplemented by extensive experiments, showed that the phenomena in question were not those of typical mutation, but are rather to be classed as striking instances of polymorphism. As, however, their interest depends in large measure, for the writer at least, upon the ease with which they may be mistaken for mutation, I will first describe the facts as they appeared in the original collection of material.

This collection was made about October 1, in the remnant of a vile pool on the alkali flat west of the city of Lincoln, Nebraska. This portion of the flat has for years been used as a dump, having been filled in several feet in depth mainly with compost. Two years previously a heavy summer flood had excavated a cavity, the size of a village lot, to the original alkali bottom, and in this cavity the pool remnant, to the depth of about one foot, remained. The water was dark brown with alkali and the essence of compost, but it suited *Asplanchna* exactly, for while almost no other plankton was present the *Asplanchnas* were so abundant as to almost touch one another; the sweep of a yard with a 20-inch dip-net brought up a double handful of the strained animals.

My original study was confined to material from this single collection because, a day or two later, a heavy rain flooded the pool, killing the *Asplanchna* to the last individual.

The collection in question contained two distinct types of *Asplanchna*. The dominant form, outnumbering the other several hundred to one, was of a large humped type, closely akin to *Asplanchna amphora*. I shall, however, postpone a detailed discussion of the species, as it is intricate, and unfortunately involves some controversy, while the interest in the phenomena which I wish to describe is not specially dependent upon it. Reference to Fig. 1 will show fairly well its general appearance, and I need but add at present that it was of very large size, frequently measuring 1,500 μ in length.

Sparsely distributed among the mass of these animals was a mammoth rotifer of related yet very different type. It was saccate, or, more truly, campanulate, in form. Its robust body, without humps, somewhat exceeded in length that of its more slender companion, while its enormous ciliated wreath or corona was extended beyond all limits that the writer ever expected to see in a rotifer. Its transverse diameter frequently equaled the entire length of the animal. This massive giant swam about with a typical though rather slow *Asplanchna* movement, vibrating or flapping first one portion and then another of the ciliated corona in a very conspicuous fashion. When it met one of the other rotifers in a head-on collision it was much less inclined to contract or turn a quick somersault than was the companion type. As to the specific, varietal, or other classification of this large campanulate *Asplanchna* I could find nothing. I concluded that it must be an as yet undescribed species. Its distinctness was further borne out by the results of detailed study.

The characters hitherto most extensively used for specific definition in the genus *Asplanchna* are size, body form, type and development of nephridium, and the form of the trophi. As to the nephridia of the two forms in question, they proved, indeed, sufficiently different. Although built upon the same general type, their size and the number of flame cells bespoke wide separation. Rousselet, who is the first authority upon the classification of rotifers, in his last article[1] discussing the species of *Asplanchna* expresses his belief that the number of flame cells is constant in each species, although he admits that it is very difficult to make strictly accurate counts of these delicate organs. He assigns to *Asplanchna amphora* about 40 flame cells, and this is a much higher number than has hitherto been found in any other species. My preparations permitted much better counts than may be made on the living animal, but still I am not certain of exactness. I found, however, that even the humped rotifers frequently bore about 50 flame cells on a side, and in many instances I found 55. In the campanulate type the number was astonishingly greater. Not only was the nephridial tube bearing the tags longer, stretching from the knotted portion near the bladder in a wide diagonal curved line to the lateral edge of the corona, but it was very thickly studded throughout the greater portion of its length with the flame-bearing tags. The number was certainly variable in larger and smaller specimens, but it was frequently about 100, and in a number of instances, by thoroughly conservative counts, I reached the surprising number of 115. The nephridial development in this giant rotifer is therefore in proportion to its large size and massive tissues. The trophi also proved sufficiently different and of a size hitherto quite unknown in the genus. A glance at Figs. 3 and 4, showing the trophi of the two types drawn to the same scale, will show at once their great difference. A detailed discussion of their minor features will show them to be still further apart.

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[1] "On the Specific Characters of *Asplanchna intermedia*," Hudson, *Jour. Queck. Mic. Club*, Second Series, Vol. VIII, pp. 7–12.

In general, then, to judge by the structure of the females, the two types seemed very distinct, and several weeks of painstaking study, including the examination of several thousand individuals, left me with very little doubt that I was dealing with what we ordinarily class as distinct species.

It was while examining some of my first mounted slides of the large *Asplanchna* that I came suddenly on the evidence of apparent mutation. As is well known, the young of *Asplanchna* are highly developed before birth, and in the material which I was studying this chanced to be true to an unusual degree. My mounted slides, too, were perfectly transparent, giving views not only of all the organs of the adult, but of every organ and almost every histological detail in the structure of the unborn young. Examining these young, I noticed at first nothing peculiar; the young within the humped rotifers bore humps even more marked than those of the adult, it being one of the recognized characters of *A. amphora* that these body extensions reach a maximum development in the young at about the time of birth. The first young noted in the campanulate type were also, in all respects, essentially like the parents.

I was, therefore, astonished to suddenly hit upon a large campanulate rotifer containing an unborn rotifer, not of its own, but of the other, the humped type, Fig. 2. The word mutation was the first thing that framed itself in the midst of my inarticulate consciousness. But of course I neither accepted at once the suggestion nor the apparent facts before me. Mutation, although among things proven, is among the things proven to be rare, and is therefore to be accepted in any given case only after fullest verification. Moreover, facts themselves are frequently deceiving. Perhaps the young humped *Asplanchna* did not belong within the body of its seeming parent. Perhaps it was some accidental inclusion forced through some invisible aperture in the side of the larger organism. In short, was it really in the uterus? Perhaps it had been swallowed by the adult campanulate and had managed afterward to tear its way through the digestive tract, which latter organ had then healed and allowed the prey to continue development in the body cavity.

While I was asking myself these questions and others, I was also assiduously seeking for more examples, for if the phenomena were regular more examples would certainly be found.

A number were indeed discovered, and every possible explanation was eliminated except that they were, as they appeared to be, young humped rotifers which were produced by normal parthenogenetic development within the giant campanulate type. I was able to discern, for some of them, that they were within the uterus, and in every way in normal position. The only slight sign of abnormality was that they usually seemed to be a little small for the parental organism producing them; they filled less of the body cavity than did corresponding young that were developed true to type. But upon second thought this was but one more sign of the completeness of the heterogenesis. These humped young were developing of exactly the size that they would have developed within the body of a humped parent; within the body of a campanulate they naturally left room, so to speak, to spare. The internal organs, too, of these heterogenetic young bore out, in detail, the conclusion suggested by the external appearance. The lighter musculature, the narrower ovary- or shell-gland, were obviously characteristic of the smaller humped type. Most definite of all, however, was the evidence of the trophi. These are universally recognized as yielding characters of specific rank. They are wholly developed before birth, and they were very different in the two types in question. I used, therefore, the utmost pains to ascertain the nature of the trophi in these heterotypic young. The result was without question; the trophi in every case indicated a complete and sudden transition from the campanulate to the smaller humped type. This was true both in regard to size and in details of structure.

I concluded, then, after the study of every organ which I could make out with clearness in the material at my disposal, that these atypic young in the large campanulate *Asplanchna* represented, not an ordinary variation, but the sudden production of one type by another and quite distinct one.

But a number of questions suggested themselves at this point. In what number were these mutants, if such they really were, being produced? Was the production of one type by the other occurring in both directions, or only in the one in which I had chanced to find it? And, again, could transition specimens or any signs of gradation between the two types be found among the adults, or individuals of any age, in the material at hand?

As to the first question, I examined carefully 270 mounted adults of the giant campanulate type. Nearly all were in reproduction, but only 90 of them contained young sufficiently advanced in development and sufficiently well placed to allow a certain judgment as to their type. Of the 90 unborn young nearly one fourth (22) were indisputably of the humped type, while 68 were just as certainly of the parental or campanulate type. Nothing should be made here of the ratio of one fourth and three fourths. The phenomena in question are not the result of a cross, and, moreover, the determination hinges upon several factors; for one thing, upon my caution, when dealing with the earlier embryos, in rejecting any case which was not quite certain. In other words, had I been working with live material and rearing the animals to a proper stage, a considerably larger proportion than one fourth would probably have turned out heterotypic.

To answer the second question—*i. e.,* whether this atypical reproduction were occurring in both directions or in one direction only—I first made a preliminary examination of several thousand individuals of the humped form, a high percentage of which contained well-developed embryos. I found no indication of any departure from normal reproduction. I then examined critically one thousand individuals, recording results in each case. Of this one thousand individuals, 419 contained young sufficiently developed and well placed to admit of safe determination. All were plainly of the parental type; nor did I find a single case in all this material that even suggested strong variation toward the larger humpless rotifer.

Transitional specimens, however, could, if present, be more certainly found among adults, or at least among individuals after birth. This was my third query. Did such exist? Throughout my entire examination I sought for them, but with little success. At certain stages in development each species approaches a little nearer to the other species. Thus the young of the larger, campanulate type are not only smaller, but have slightly bulging sides, suggesting the possibility of humps. Their corona, too, although very heavy and broad, is less disproportionately so than in the fully grown adult. But in no case was it difficult to determine the relationship of such specimens; other characters placed them at once, especially the enormous and differently formed trophi, which are fully developed before birth. Very old adults of the smaller humped type might possibly, at first glance, be taken for variants toward the larger form, in that their humps become smaller and less sharply marked off from the general body wall. In no other character, however, do they approach the campanulate type. Putting aside such stages, which, with a little practise, fall naturally into place, the amount of further variation did not prove to be great. The humps, both lateral and ventral, on the smaller type, did show a considerable amount of variation in relative size. And in numerous cases it was of interest to note that such variations were plainly hereditary; *i. e.,* an extra large female with, say, relatively small humps, would contain a large young individual that was obviously of the same type.

But these minor variations were to be expected; as well as their tendency toward transmission, but they had no evident connection with the type of change of which I was in search.

Of true transitional types I discovered but two possible instances. These two individuals were quite alike, but differed notably from any others of the thousands studied. Each was, all in all, indisputably a humped rotifer, but decidedly beyond the ordinary maximum size and with disproportionately small humps. The corona of each was much broader and its cells much heavier than in any other humped individuals observed; the body walls and musculature also were much heavier, taking the deep stain shown otherwise only by the campanulate. All of these characters approached more or less the campanulate type. Most striking, however, were the so-called ovaries. In each case they were of the heavy type shown by the larger rotifer. The nephridia did not admit of careful observation. The most crucial organ of all, however, the trophi, agreed wholly with the humped type in form, and, though large, did not exceed the maximum size found in the ordinary type. Studying these two individuals with care, I came at last to the conclusion that, although in a sense they might be called transitional, they were after all only variants of the humped type—variants pointing toward, but not actually leading to, the production of the campanulate type.

All in all, then, my search for signs of genetic relationship between the two types seemed to leave the evidence for mutation sharp and clear: the transition from the giant humpless *Asplanchna* to the smaller humped type was sudden and complete; it involved many characters; it was being effected in many individuals simultaneously; it was a transition in one direction only; intermediate types and fluctuating varieties seemed, in all the material studied, no more in evidence than was to be expected in any two species of one genus. At the close of this part of my study it seemed that I had found an ideal case of mutation, agreeing in every particular with the definitions of the concept put forward by its originator, DeVries.

However, just as I was finishing the study of the preserved material at hand, and deeming that I had reached the above conclusions with full certainty, I was suddenly halted by coming into possession of more living material, and material so surprising that my well-worked-out results again assumed the character of problems, and I resolved, if possible, to subject the whole to the test of experimental method and further observation.

It was about the middle of March, 1910, that the *Asplanchna* began hatching in a large covered aquarium jar in which I had placed some of the resting eggs the fall before. Between the last of March and the 10th of April the species also began to appear gradually in two ponds, in which, fortunately, the available food organisms for many weeks were wholly different. Observations were thus begun upon the species under diverse conditions, even from the start. And, as they were continued with but few and short interruptions through the spring, summer, and well into the succeeding fall,[2] the variety of conditions under which the development of the species was followed included very wide extremes. Thus, during a cold period in early April the species multiplied in shallow ponds upon which ice was forming nearly every night, while heavy prevailing north winds kept the water in continual turmoil. On the other hand, in July and August, I was able to study the species in both permanent and temporary ponds during periods of the hottest summer weather.

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[2] Since the above was written nearly all of the phenomena recorded have again been observed during a second season.

Side by side with these observations, and correlated with them as far as possible, a large number of culture experiments were carried out.

The general method was as follows: The ponds were visited several times a week, and such observations as possible made on the spot. Then large quantities of the animals, together with their food organisms, were brought to a basement laboratory and placed in large aquarium jars. These mass collections were sometimes obtained by merely dipping up the water and the organisms it contained in their natural degree of dispersion; at other times the organisms were much concentrated by the addition of large numbers taken with suitable nets. Few results were more interesting than the observation of the resulting phenomena in parallel aquaria in which the animals had been placed, now in small numbers, and again in various degrees of concentration up to almost actual contact.

The material in these mass cultures was critically examined and followed from day to day. Then, whenever interesting phenomena seemed to be occurring, either in the ponds or the mass cultures, or in both, isolation experiments were begun with single individuals, or with a definite number carefully selected and examined one by one.

To my satisfaction, the animals proved remarkably adapted to experimental treatment. They withstand a great variety of environmental influences, providing only that two conditions are rigidly met. In the first place, a copious food supply must be furnished; and second, the fluid medium (it may be saturated with such ingredients that one hardly speaks of it as water) in which the animals have developed must be left practically unchanged. This latter condition limits the range of possible experiment, but I could not once succeed in getting *Asplanchna* to live and reproduce in any other than its native fluid;[3] even dilution of one fourth with water from some other source seemed in every case to preclude a successful culture. In nature, too, every rain which diluted to an appreciable extent the vile ponds in which this *Asplanchna* flourishes results in the death of the entire stock, which is only replaced by the hatching of new individuals from resting eggs.

As to food, many organisms were tried, and a number proved available. Best of all, for the smaller forms of the *Asplanchna, Paramecium* proves an ideal food. Other rotifers come next, of which I used especially *Hydatina* and *Brachionus;* while, surprising as it would appear, the crustacean, *Moina paradoxa,* although a large-sized member of its group, provides, under certain circumstances, an available food supply for this overgrown and voracious rotifer. The adult *Moinas* are not eaten, but young and even half-grown individuals may be regularly eaten by the mammoth campanulate form I have described. The humped rotifers ingest the crustacea with difficulty, but succeed in doing so at times to a considerable extent.

Omitting further reference to methods, and refraining from any attempt to describe the course of experiments, I will briefly give their results, prefacing only that I make no general statement which is not based on the outcome of at least ten separate experiments or as ample observations in nature, or on both.

The first of these results which I will state, although nearly the last that I demonstrated, is the error of my original conclusion in regard to the relationship betwen the two types already described. The campanulate and humped types do reproduce each other reciprocally, although with very different frequency in the two directions. Moreover, transition forms (in every feature except the trophi) do occur between them under given though unusual conditions. The phenomena thus fall more naturally under the rubric of dimorphism than under that of mutation; although, as will be apparent later, the phenomena with this rotifer bring the two concepts into closer relation than they have perhaps ever been brought before.

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[3] This does not apply to cultures started from resting eggs. These may be hatched and the young developed in varied media.

The second general result of work with the living animals was the surprising discovery that the species is not only markedly dimorphic, but trimorphic, possessing a third form—a smaller saccate type which differs from both the humped and the campanulate types quite as much as these differ from each other, and which, curiously enough, differs far more, in external appearance at least, from these other forms of its own species, than it does from an allied but distinct species, *Asplanchna brightwelli.*

I shall return to this latter point of specific distinctness again. But by way of description I will here state that this saccate type, as I shall call it, although showing a considerable range of fluctuating variability, is a rather primitive but typical *Asplanchna.* In size it averages much smaller than either of the other types dealt with, reproductive individuals ranging from about 500μ to 1,200μ in length. In outward form it resembles closely, now *A. brightwelli,* now *A. priodonta.* The corona, when the animal is seen from the end, is always circular, as is typical for the genus, never showing the strong dorsoventral flattening which is the invariable condition in the humped and campanulate types. Correlated with this circular corona is the general cylindrical shape of the animal. When placed on a slide in a shallow drop of water these saccates characteristically rest on their sides instead of their dorsal or ventral surfaces as do both of the larger types. The trophi are of the same type as are those of the humped *Asplanchna,* except that they are a little smaller and proportionally a little more robust.

The internal organs are of the same general character, although more compact and filling more of the body space than in the two larger forms, two of them, however, being notably different in development.

First, the nephridia. I have not studied these in stained preparations as I have in the other types, but, using living material, I make out a decidedly variable number of flame cells; they range from as low as twenty to nearly forty. It is at least plain that the number averages much less than in the humped form, and but a fraction of that in the campanulate. The difference would seem to be plainly correlated with the general differences in the size of the organisms.

Singularly in contrast to the smaller nephridia is the development of the contractile vesicle or bladder. This is a small organ in both the humped and campanulate types, but in the much more diminutive saccates it becomes very much larger, filling, when expanded, a large part of the body cavity. I have examined considerable numbers from diverse sources and reared under different conditions, to make sure that this contrast was not accidental. I find no exceptions to it. Like the number of flame cells, this matter of size of the contractile organ, relative to that of the body, has been hitherto considered a specific difference.

A final peculiarity of the saccate type, although a variable one, is its tendency toward an excessively rapid rate of parthenogenetic reproduction; it is usually crowded with embryos. Four, five and six are frequent; sometimes I have counted nine; while in many individuals they are so closely packed that counting is out of the question. These numerous young are also frequently born at a disproportionately small size, even compared with the diminutive parent, thus still farther increasing the extremes of size which the species presents. It seems probable that this smaller and less developed type is itself, to some extent, a product of this rapid rate of multiplication. I have found it multiplying at a slower rate—*i. e.,* producing but one or two embryos; but such instances were always due to degeneration or growth under unfavorable conditions. I may add by way of contrast that the humped form most typically produces but one young at a time. Thus, in the material of my original study, among one thousand individuals I found but sixteen showing the more or less simultaneous development of two embryos, and none showed more than two. The campanulates regularly develop several embryos at once, four and five being common numbers; but in their capacious bodies there is no overcrowding, and certainly no curtailment of nutrition.

As to the occurrence, the definite relationship, and the causes of the production of the three types of the species, I have ascertained most of the facts, though not all.

The saccate form is, I think, unquestionably the only form that emerges from the resting egg. In all cases—seven in number—in which I have examined temporary ponds within a few days after formation and found this rotifer just appearing, or in which I have caught the species evidently close to its first appearance, I have found either nothing but the saccate type, or numerous saccates, together with transitional and humped types. In the majority of these cases the saccates have been rapidly displaced by the humped type, which, in nature at least, very rarely reverts to the production of the smaller form. As soon as the species is in full swing, so to speak, countless numbers may be examined for weeks without a saccate occurring. All of these phenomena have been paralleled in my aquaria, and I have also repeatedly observed the birth of the humped type from the saccate parent. This is usually in instances where the high numbers of developing embryos in the saccate parent have given place to few or to but one. Usually, too, the parent is a rather large saccate and the humped young a rather small example of its type. But occasional instances have been noted where the humped young, a moment after birth or as soon as it had assumed complete expansion, appeared fully a third larger than its saccate parent. The act of giving birth to such heterogenetic issue is a decidedly prolonged and painful process for a rotifer, very different from the ordinary, sudden expulsion, well known in *Asplanchna.*

Turning to the consideration of the actual cause of the transition from the saccate to the larger humped form, I have not discovered it definitely. The cessation of the rapid rate of reproduction, already spoken of, seems a partial proximate cause, though it itself I can not explain. It seems in part a mere matter of the number of generations following hatching from the resting egg. But a copious food supply and generally favorable conditions probably favor the change. In early spring the saccate form maintained itself for several weeks in a pond where, in July, after drying up and being refilled by rain, the saccate form began to produce the humped form sparingly within four days, and was very soon supplanted by it. In another pond of purer water and seemingly less well adapted to the species, the saccate form appeared scantily in early May, and struggled on sparingly for three weeks, feeding mainly upon the flocculent masses of blue-green alga, but somewhat upon *Brachionus;* it then disappeared entirely, having produced no form but its own so far as I could discover. Yet in isolation cultures from this same stock, when fed on *Paramecium,* I raised, after several generations, a number of rather small humped *Asplanchna.*

While I have seen little evidence, thus far, that either of the larger types give rise to the saccate form in nature, yet in two small cultures I have produced a population of from one hundred to several hundred small saccates by the degeneration of the humped stock. In one case the colony was a very old one and the degeneration possibly due to this fact; in the other it was plainly the result of diluting the culture medium with tap water. The small saccates, even when they had dwindled to a half dozen, before total lapse, still bore developing embryos in their diminutive bodies.

The typical case of relationship, however, is, plainly, for a few generations of rapidly developing saccates to be succeeded, after a few transitional forms, by a continuous and ever-increasing population of the humped type.

As to the occurrence of the humped type, this is, practically, as just stated. Although never hatching from the resting egg, it soon supplants the smaller and earlier form and then continues to multiply, in favorable localities, until put an end to by drought, rain, or the exhaustion of the food supply. I do not believe that it can multiply indefinitely, however, for in even my largest aquarium jars, the species invariably seems to die out after several crescendos and decrescendos of development. The largest cultures have lasted about five months. That their death is not due to the accumulation of metabolic products in the unchanged water seems probable, because in one case a new generation hatched from resting eggs soon after the death of the first, and showed no signs of weakness, although growing in the same long-used medium.

The occurrence of the giant campanulate form is a totally different matter from that of the other two types. It never occurs alone. It never occurs in newly hatched cultures or young stocks.[4] It rarely occurs in great numbers, and never does it do so, so far as I have ascertained, in nature when feeding upon what may be called a normal food. On the other hand, in old stocks that have become numerous, I find this giant type invariably present. The original collection which I studied was about typical in this respect. I have not ascertained the exact proportion which the campanulates bear to the humped form in any given case, for experiment shows that it is capable of variation within wide limits; but I think that in nature they would rarely equal one to one hundred.[5]

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[4] This holds good under all ordinary conditions. Since the above was written, the experiment has been made of hatching out hundreds or thousands of resting eggs in a very small space—*e. g.*, a three-oz. bottle, in almost pure tap water. The results of this experiment are very striking. Placed thus from the start almost without nutrition, a few of the more vigorous animals begin cannibalism at once, with the result of a very early appearance of both the humped and the campanulate types. In just what generation they thus appear is not known, but very probably in the second and third respectively. The development and saltation occur with but few individuals, the majority starving to death or serving for food only.

What was the relation of these two types? Weeks of all but continuous work were necessary to decipher it. The fact that the two types were so frequently associated indicated probable connection, but did not demonstrate it; the fact that the campanulate always appeared only long after the development of the humped form was again suspicious, but proved nothing. Isolation cultures of the campanulates soon showed, as my mounted material had done, that they regularly produced not only their own type, but a considerable proportion of the humped type as well. But the reverse process is at least so rare that I have been as unable to find it among my living material, as I was among that which I had mounted. Scores of isolation cultures, begun with few or single individuals, fed on diverse types of food, and nearly all very successful, remained negative in result, with the exception of one of my very first attempts. I was trying out the rotifer, *Hydatina,* as a possible food for the humped *Asplanchna,* and placed half a dozen of the ordinary type in a watch-glass with many of the smaller rotifers. Soon, among the young produced, there appeared one that rapidly developed into the giant type; but subsequent trials, carried on as long as this special food supply lasted, were negative in results.

Over against these failures, however, a large number of my mass cultures yielded at once *all but* conclusive evidence that the larger type was somehow derived from the smaller. These cultures were started as follows:

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[5] During the recent summer one pond in which the species developed copiously from spring to August showed at the latter period a much higher number—about one campanulate to 20 humped.

From the surface of a pond several feet in depth, and at a point several feet from the shore, a large quantity of the humped type were collected with a small net. This material and the entire pond, so far as my investigations had gone at this time, had shown none of the larger form, and the care with which the material was taken from the surface rendered it improbable that a resting egg of the larger form should contaminate it, the resting eggs of all these rotifers being heavy and sinking at once.[6] This material was placed in clean transparent jars of several liters, although beside each larger culture was usually placed a smaller one in a tall thin vessel which permitted careful scrutiny of the entire contents with a low-power lens. It was almost impossible to crowd the animals to the point of injury, though perhaps every other visible organism would die. Now in all of these crowded mass-cultures, whether large or small, whether fed, half-fed, or starved, the campanulate form made its appearance within at most a week. Sometimes a single individual, either young or fully developed, would first be discovered; more frequently a number would be present before noticed. But in every instance the sudden appearance of the large form was followed by its very rapid multiplication, coincident with a still more rapid diminution in numbers of the humped form. The latter were eaten up by the former, even adults of the humped type falling victims to the prodigious ingesting power of the campanulates. This all but complete displacement, in the course, say, of three weeks, of one form by the other, was a striking and almost astonishing spectacle. I have not observed it in nature, however crowded the species becomes in its natural situation. But in my culture dishes it was the regular occurrence in case the individuals became sufficiently numerous.

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[6] It has later been ascertained that, under certain circumstances, some of the resting ova may again rise and float; in a windy pool, however, they would very soon be blown to the margin and lodged. Yet the force of the experiments cited is reduced.

The suggestion of cannibalism as the cause was thus all but conclusive; but I was able to press the proof one step farther. My isolation cultures, started with one or a few individuals, invariably failing, I decided to try cultures started with a larger number of individuals, each one of which was first subjected to examination under the microscope. 240 individuals were thus isolated and placed in a single stender dish, care being taken to reject any that deviated never so little from the normal humped type, especially as to extra size. In the rapidly multiplying culture thus started there appeared within a week several typical campanulates, and the whole subsequent course of the culture duplicated the developments which had taken place in the mass cultures already described. This is as near as I have come to actually observing the production, by the humped *Asplanchna,* of its larger humpless congener. I have not witnessed the birth of the one from the other or seen it in uteri. The demonstration of fact is, however, sufficiently complete, and the farther conclusion is sufficiently plain, viz., that the transition in this direction between the two types is a relatively rare one. Not every humped *Asplanchna* possesses the power, whether this depends upon size, ingestive reaction or digestive capacity, to produce the larger form. Indeed, this power would seem to reside in but very few individuals.

As soon as I had reached even the tentative conclusion that cannibalism must be the cause of this marked heterogenesis, I set about to determine, if possible, why this should be the case. Was there some magic in the cannibalistic diet as such? Was it merely a case of rich nutrition? Or was the result perhaps due to the mere size of the ingested food organisms?

Excessive feeding with most of the usual food organisms of the species was plainly without result. So long as the *Asplanchnas* were relatively few or greatly outnumbered by their food organisms they glutted themselves to repletion without unusual consequences in reproduction. Thus in the case of one pond, an algal-feeding *Brachionus* developed until it exceeded in numbers anything that I had ever before observed under similar conditions. The surface water was so filled with them that one observer pronounced it as thick as good tomato soup. In this medium the humped *Asplanchna* gorged itself during days of rapid multiplication. Every stomach was packed with the smaller rotifers; yet no change in type resulted. Finally the *Asplanchnas* literally ate up the *Brachionus,* but themselves disappeared a short time after this was accomplished without having produced any of the giants. Yet condensed material taken from this same source and placed in large culture dishes did produce the cannibals some time after the *Brachionus* had been devoured. It follows from this instance, as well as from a number of others equally conclusive, that mere feeding on the flesh of rotifers, so to speak, is not sufficient to cause the change.

The same proved true of over-feeding on *Paramecium* and several other protozoa that were greedily eaten.

I was the more surprised, therefore, to discover one other food organism, and one only, so far as my observations extend, which is fully competent to bring about the same result. It is the Daphnid-like crustacean, *Moina paradoxa.* It seems almost incredible that a rotifer should feed upon this robust entimostracan, even the young of which are born of a size which would seem beyond the utmost stretch of a rotiferean stomach. Moreover, this *Asplanchna* does not by any means invariably attack *Moina.* It may disappear, seemingly from starvation, in a pond where *Moina* is present and rapidly multiplying. This has also happened repeatedly in my cultures, and I have placed numbers of the young *Moinas* in watch-glasses together with the *Asplanchna* without having them eaten. Yet in other very similar cases the young *Moinas* are ingested by the *Asplanchnas*—by the humped form, and rarely by the larger saccates. The very youngest *Moinas* may even at times be ingested by the smaller saccates. It seems probable that the vigor of the *Asplanchna* stock, and, I think, the period in the reproductive cycle (number of generations since the resting egg), have much to do with the refusal or attack of this oversized food organism. Be this as it may, however, the habit of eating the young *Moinas,* once started, seems to rapidly become fixed in not only the individual, but its progeny and the whole subsequent stock; although, weeks later, perhaps, this feeding reaction may again be lost, and the last rotifers starve to death in the presence of abundance of young *Moinas.* Such starving stocks may be again revived, when almost perished, by the supply of a smaller food organism.

Now the feeding upon this crustacean has, to all appearance, the same effect in bringing about the production of the large campanulate type as has cannibalism. I have not proven it with the same precision, but I have observed the transformation of mass cultures from the smaller to the larger type under circumstances that suggested the all but certain conclusion that *Moina*-feeding was the initial cause. I have also reared large numbers of the campanulates, for weeks at a time, by using the young *Moinas* as food. Under these circumstances the humped rotifers all but disappear from the cultures. A few always remain, because they are continually being produced, in minor numbers, by the campanulate type. But as very few of the humped young are able to acquire the habit of *Moina*-feeding, they starve to death without reproduction or fall victims to their mammoth progenitors.

In one instance, and one instance only, I have followed the transformation of the *Asplanchna* to its largest type, through *Moina*-feeding, in nature. The case interested me much, being very different from any other instance that I have followed, and showing to an astonishing degree the protean possibilities of the species. As usual, the first appearance of the species was in this instance by scattered individuals of the saccate form. Their food consisted chiefly of *Brachionus* and *Hydatina*. These organisms were not numerous, however, and were exhausted just as the countless hordes of the young *Moinas* appeared. Under these circumstances a wholesale transition to *Moina*-feeding occurred, even while the *Asplanchna* was in its earlier phases of development. The smaller humped forms had just begun to appear when the *Moina*-feeding began, both by these humped individuals and by not a few of the larger saccates. The species became for a few days indescribably chaotic. So far as body form was concerned, transition stages could be found between every possible type and variation. This is the only instance in which I have found the saccate form giving rise to the campanulate without the humped intermediate, but it certainly did so to a considerable extent in this case. The outcome of *Moina*-feeding in this pond was the establishment, after about nine days, of a new equilibrium for the species. The giant campanulates had become in this instance, and this instance only, among my observations in nature, the preponderant type, reproducing their own form in the main, but also a few slender, long-humped individuals. Of these latter a very few managed to ingest the *Moinas* and to reproduce, while the majority showed empty, shrunken stomachs and no developing embryos. All traces of saccate and transitional forms had disappeared.

I will note, in passing, that the campanulate form which is produced by the *Moina*-feeding is not quite identical with that procured by cannibalism. The size reached is even a little larger, and the animals have the appearance of being even more powerful in general musculature; but the flaring corona never becomes quite so extreme; the animals never assume quite the bell-like form which the most majestic cannibals present.

(*To be concluded*)